Original Article

Sexual and size dimorphism in two deep-water hermit crabs (Decapoda: Parapaguridae) from the Western Atlantic Ocean

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ABSTRACT

The Parapaguridae comprises hermit crabs that inhabit deep-water environments. In these environments, shell availability can be limited, mostly consisting of small and fragile-shelled gastropods. Thus, different strategies have evolved to mitigate this limited shell supply. *Sympagurus dimorphus* (Studer, 1883) lives in association with a zoanthid cnidarian that creates a pseudo-shell that grows with the hermit crab. In contrast, *Oncopagurus gracilis* (Henderson, 1888) inhabits small, calcified gastropod shells. Therefore, we selected these two species as models to test sexual dimorphism and shape patterns of their chelipeds and cephalothoracic shield, due to their different shelter acquisition methods. We photographed the animals and digitized the images to employ comparative geometric morphometric techniques. We tested the differences in shape between the sexes within each species, and also tested sexual size dimorphism based on centroid size. For *O. gracilis*, we found shape differences for the chelipeds and cephalothoracic shield, however, we only observed sexual size dimorphism for the chelipeds. For

S. dimorphus, an inverse pattern was found, in which females presented more robust chelipeds, and sexual size dimorphism was present in which males were larger. These differences can be reasonably explained by their shelter acquisition methods, in which *O. gracilis* depends on small shells that limit growth, while *S. dimorphus* grows with its cnidarian pseudo-shell. The robustness found in the shape patterns may also be related to their behaviors, e.g., in addition to competition for shells, they also fight during mating. However, we emphasize that future studies with other populations of these species are needed for comparative purposes.

INTRODUCTION

The Parapaguridae comprises hermit crabs found in deep waters ranging from 100 meters to over 4000 meters, with a cosmopolitan distribution (Schembri and McLay, 1983; Lemaitre, 2004; Cardoso and Lemaitre, 2012; Olguín et al., 2014). Currently, there are ten genera described for this family (Lemaitre and McLaughlin, 2023), however, information on the biology of this group is scarce, mainly due to sampling difficulties (Olguín et al., 2014). Gathering information on the biology and ecology of fauna inhabiting deep waters is an expensive and challenging task.

Acquiring basic biological information, such as population studies, can improve species knowledge and help inform management and conservation strategies (Keunecke et al., 2007; Capparelli et al., 2012; Silva et al., 2013; Ulman et al., 2022). Morphological studies offer insights into behavior strategies and energy allocation both between and within species and populations (Hartnoll, 1974, 2001; Davanso et al., 2017; Gonçalves et al., 2017). Additionally, morphological and morphometric studies aid in understanding phenotypic evolution (Oliveira and Custódio, 1998; Allen and Levinton, 2007; Dennenmoser and Christy, 2013; Lunt et al., 2017; Levinton and Weissburg, 2021; Nogueira et al., 2022; Painting, 2022).

Hermit crabs, with their unique non-calcified abdomen, rely on external structures for cover and shelter (Williams and McDermott, 2004), with empty gastropod shells being the most commonly used resource (Vance, 1972; Kellogg, 1976; Bertness, 1981). Within the Parapaguridae, *Sympagurus dimorphus* (Studer, 1883) is a widely distributed species in the southern hemisphere, inhabiting depths ranging from around 90 to 1995 meters (Lemaitre, 2004; Landschoff and Lemaitre, 2017), and frequently associated with zoanthid cnidarians that build a pseudo-shell, rather than inhabiting empty gastropod shells (Schejter and Mantelatto, 2011). Linear morphometrics and population studies have been recorded for *S. dimorphus* on both margins of the South Atlantic Ocean (Schejter and Mantelatto, 2015; Schejter et al., 2017; Wright et al., 2020a; Wright et al., 2020b). *Oncopagurus gracilis* (Henderson, 1888) is another parapagurid with a wide distribution, inhabiting depths ranging from 146 to 900m in the Western and Eastern Atlantic (Merchán-Cepeda et al., 2009; Lemaitre and Tavares, 2015). Unlike *S. dimorphus*, *O. gracilis* utilizes vacant gastropod shells as shelter (Lemaitre, 2014). Despite its broad distribution, little is known about the biology of *O. gracilis*.

Decapod crustaceans exhibit a range of behaviors during resource disputes with their conspecifics. These agonistic events may involve the use of claws, which can serve as signals or weapons to injure opponents (Mariappan et al., 2000). Sexual dimorphism is often found in crustaceans, in which males are usually bigger than females (Oliveira and Custódio, 1998; Turra and Leite, 1999; Diawol et al., 2015), and when the sexual dimorphism is found in chelipeds, these structures are often bigger and stronger than those of females (Doake et al., 2010; Copatti et al., 2016; da Silva and Nogueira, 2023); as seen for several anomuran (Turra and Leite, 1999; Trevisan et al., 2012; Copatti et al., 2016), and brachyuran species (Abelló et al., 1990; Tsuchida and Fujikura, 2000; Marochi et al., 2016). However, crayfish that live in constant intersexuality,

such as representatives of the genus *Parastacus* Huxley, 1879, do not exhibit sexual dimorphism (Almeida and Buckup, 2000; Silva-Castiglioni et al., 2008; Palaoro et al., 2013).

Despite having smaller claws, females also engage in resource competition using these structures (Briffa and Dallaway, 2007; Dalosto et al., 2019; Rappaport and Lord, 2021). Dimorphic traits have been analyzed in hermit crabs from the families Paguridae and Diogenidae, and it has been observed that males tend to have larger body sizes and weapons (claws) than females (Briffa and Dallaway, 2007; Yasuda et al., 2017; Nirmal et al., 2020). Despite this, information on the biology, morphological traits, and sexual dimorphism of the Parapaguridae remains scarce. Acquiring knowledge about the shape and biomechanics of weapons in hermit crabs is crucial since their claws are essential for competing for various resources, including food, sexual partners, and shells (Dowds and Elwood, 1983). During fights, especially for shells, hermit crabs use chelipeds to hold and hit an opponent's shell in a series of bouts (Lane and Briffa, 2020; Lane et al., 2022), thus a biomechanically efficient claw assures a firmer grip in order to perform these actions with proper accuracy. However, the morphology of the claws in *S. dimorphus* may deviate from the general pattern observed in other hermit crab species. This is because these crabs have adapted to using a different type of living shelter, which is a structure called a carcinoecium. The carcinoecium is constructed from a living colony of the cnidarian *Epizoanthus paguricola* Roule, 1900, that mimics the internal structure of a gastropod shell (Schejter and Mantelatto, 2011). Schejter and Mantelatto (2011) hypothesized that the major cheliped, which closes the aperture of this pseudo-shell, much like a gastropod operculum, may serve as a template for the configuration of the growing aperture edge. Thus, this species does not need to engage in constant fights for shells, since the zoanthid grows with the hermit crab, so its claws could be selected to optimize other behaviors rather than fighting. In other hermit crab species, shell fighting behavior can select certain morphological traits (Yasuda et al., 2011; Yoshino et al., 2011). On the other hand, *O. gracilis* occupies gastropod shells of the genus *Turris* Batsch, 1789 (Henderson, 1888).

Unlike *S. dimorphus*, it is expected that *O. gracilis* engages more frequently in agonistic behaviors to acquire better-fitting shells as it grows, therefore its claws could be selected for traits to increase the chances of acquiring best fitting shells.

Given the potential differences in resource acquisition behaviors between these two species (*i.e.*, *S. dimorphus* and *O. gracilis*), variation in the development of sexually selected traits may occur. When occupying poorer-fitting shells, hermit crabs may not achieve bigger sizes compared to those using best-fitting shells (da Silva et al., 2019); also when using non-dextral shells, the morphology of chelipeds, uropods and pleopods may change (Imafuku and Ikeda, 2014). Consequently, we have selected these two species to investigate and compare the patterns of sexual dimorphism and shape variation in two crucial structures for hermit crabs: the cephalothoracic shield and claws. In *S. dimorphus* the shell competition is low due to the use of a constant-growing shelter (zoanthid carcinoecium), whilst, in *O. gracilis* the shell competition is higher and shell availability in deep sea environments may be limiting (Absalão et al., 2005; Figueira and Absalão, 2010; Abbate et al., 2022).

Thus, our hypothesis is that there will be differences in the size and shape of these selected traits between the two species. It is expected that more pronounced sexual dimorphism will be found in species that frequently engage in competitions for shell resources, leading to more significant selective pressures. Conversely, in species with reduced shell competition, selective pressures may be lower, resulting in similar sizes and weaponry between males and females.
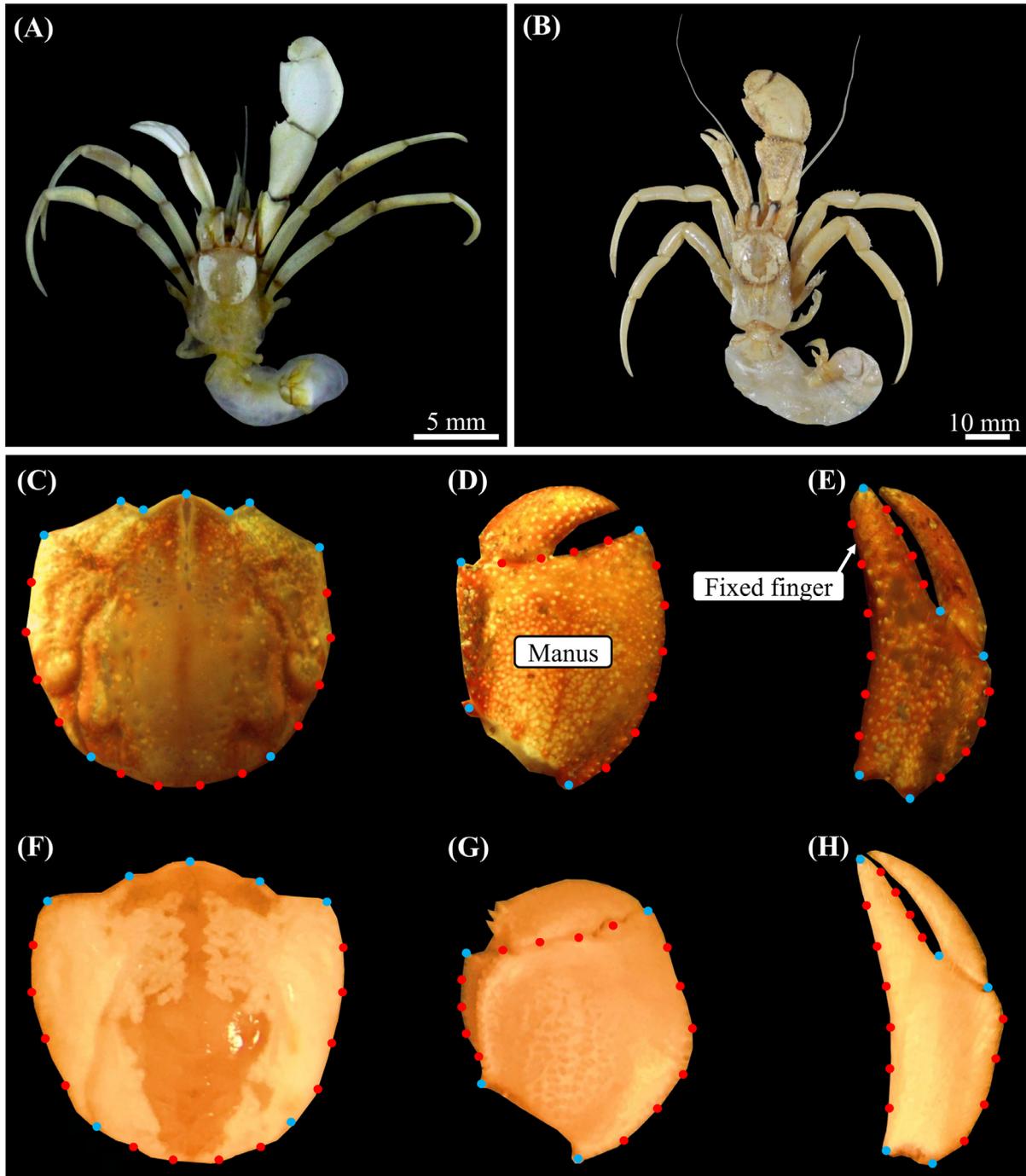
MATERIAL AND METHODS

Data Acquisition

Specimens of the hermit crab *O. gracilis* (Fig. 1A) that were used in this study are part of the Carcinology collection at the Zoology Museum of the University of São Paulo (Lots – MZUSP 16810 to MZUSP 16812, MZUSP 16817, MZUSP 16819, MZUSP 16825, MZUSP 16828, MZUSP 16829, and MZUSP 16831). According to the collection information, the animals were all collected in 1987 in the southeastern region of Brazil, between approximately 19°36'S 38°53'W to

23°46'S 42°09'W, at depths ranging from 500 m to 785 m. The specimens of the hermit crab *S. dimorphus* (Fig. 1B) were collected in 2017 in Argentina, specifically in the shelf-break front area, at approximately 39°S and 100 m deep during scientific expeditions that were focused on the stock assessment of the Patagonian scallop *Zygochlamys patagonica* (P. P. King, 1832).

Voucher specimens used in this study were deposited in the Carcinology collection at the Zoology Museum of the University of São Paulo (MZUSP 42442).

For the geometric morphometric analyses, 81 individuals of *O. gracilis* (41 males and 40 females) and 47 individuals of *S. dimorphus* (17 males and 30 females) were used.

Figure 1. Specimens of **(A)** *Oncopagurus gracilis* (Henderson, 1888) and **(B)** *Sympagurus dimorphus* (Studer, 1883). **(C)** Cephalothoracic shield, **(D)** Major propodus, and **(E)** Minor propodus of *S. dimorphus*. **(F)** Cephalothoracic shield, **(G)** Major propodus, and **(H)** Minor propodus of *O. gracilis*. The blue and red dots represent the digitized landmarks and semi-landmarks in each structure, respectively.

Geometric morphometrics

We analyzed three different structures, namely the cephalothoracic shield (CPS), and the major (MaP) and minor propodus (MiP) of the chelipeds. These structures were selected because they exhibit variation in size and shape between males and females of several hermit crab species (Briffa and Dallaway, 2007; Yasuda et al., 2017; Nirmal et al., 2020). *Oncopagurus gracilis* and *S. dimorphus* exhibit patterns of heterochely and handedness, wherein one claw is larger than the other (heterochely), and the larger claw is always on the same side of the body (handedness). Accordingly, MaP and MiP correspond to the right and left propodi, respectively.

The photographs employed in the geometric morphometric analysis were captured using a Canon T6 camera fixed on a tripod, carrying an 18–55 mm lens. All photographs were taken by the same person. In addition, the distance between the lens and structures, the zoom constancy, and the position of the structures were standardized in all photos (sensu Viscosi and Cardini, 2011).

Landmarks and semi-landmarks were digitized to characterize the CPS, MaP, and MiP shapes. The number of digitized landmarks and semi-landmarks between species was different due to interspecific morphological variation. In *S. dimorphus*, 9 landmarks and 12 semi-landmarks were digitalized in CPS, 4 landmarks and 10 semi-landmarks in MaP, and 5 landmarks and 14 semi-landmarks in MiP (Figs. 1C, 1D and 1E). In *O. gracilis*, 7 landmarks and 12 semi-landmarks were digitized on the CPS, 4 landmarks and 14 semi-landmarks on MaP and 5 landmarks and 14 semi-landmarks on MiP (Figs. 1F, 1G and 1H). All landmarks and semi-landmarks were digitized using tpsDig 2.1 and tpsUtil 1.26 software (Rohlf, 2004; 2006). The semi-landmarks were slid to reduce the bending energy and avoid unreal deformations of the structures, due to the non-homologous nature of the semi-landmarks. This procedure was performed using the tpsUtil 1.6 software (Perez et al., 2006; Gunz and Mitteroecker, 2013).

The variables that describe the CPS, MaP, and MiP shapes (weight matrix) and the centroid size (CS) were obtained using the tpsRelw 1.49 software (Rohlf, 2010) after Generalized Procrustes Analysis (GPA). The CS is a multivariate measure that describes the size of the analyzed structure and is defined as the square root of the sum of the squared distances of each anatomical landmark and the center of mass of the structure (Bookstein, 1997).

Data analysis

A principal component analysis (PCA) was performed with the weight matrix variables to check how many and which components explained more than 99 % of the data variation. Subsequently, only those components were utilized in the analysis of shape variation between males and females. This method was used to reduce the dimensionality of the data matrix and increase the power of the statistical test without losing the representativeness of the shape variation of the structures (Mitteroecker and Gunz, 2009).

To evaluate the degree of sexual shape dimorphism between males and females of both species, Hotelling T^2 tests were performed, followed by discriminant analyses to determine whether the sexes could be differentiated based on the shape of the structures. The software tpsRegr 1.31 was utilized to represent the shape of the structures associated with the axes of the discriminant analyses (canonical variables) (Rohlf, 2009). Sexual size dimorphism was assessed using the centroid size as a proxy for size. The centroid size of males and females of both species was compared using a *t*-test ($\alpha = 0.05$), prior to this step the data were checked for normality and homocedascity to account for the statistical premises. All analyzes were performed in R (R-Core Team, 2023).

RESULTS

Oncopagurus gracilis

The shape of CPS (Hotelling $T^2 = 98.62$, $F = 4.28$, $p < 0.001$), MaP (Hotelling $T^2 = 68.77$, $F = 6.83$, $p < 0.001$), and MiP (Hotelling $T^2 = 79.43$, $F = 5.7$, $p < 0.001$) were different between male and female individuals. The discriminant analysis accurately classified 90 %, 82.05 %, and 82.72 % of individuals based on their CPS, MaP, and MiP shape, respectively.

The shape of the CPS of females was observed to be wider anteriorly than that of males (Fig. 2A), while the posterior margin of this structure was wider
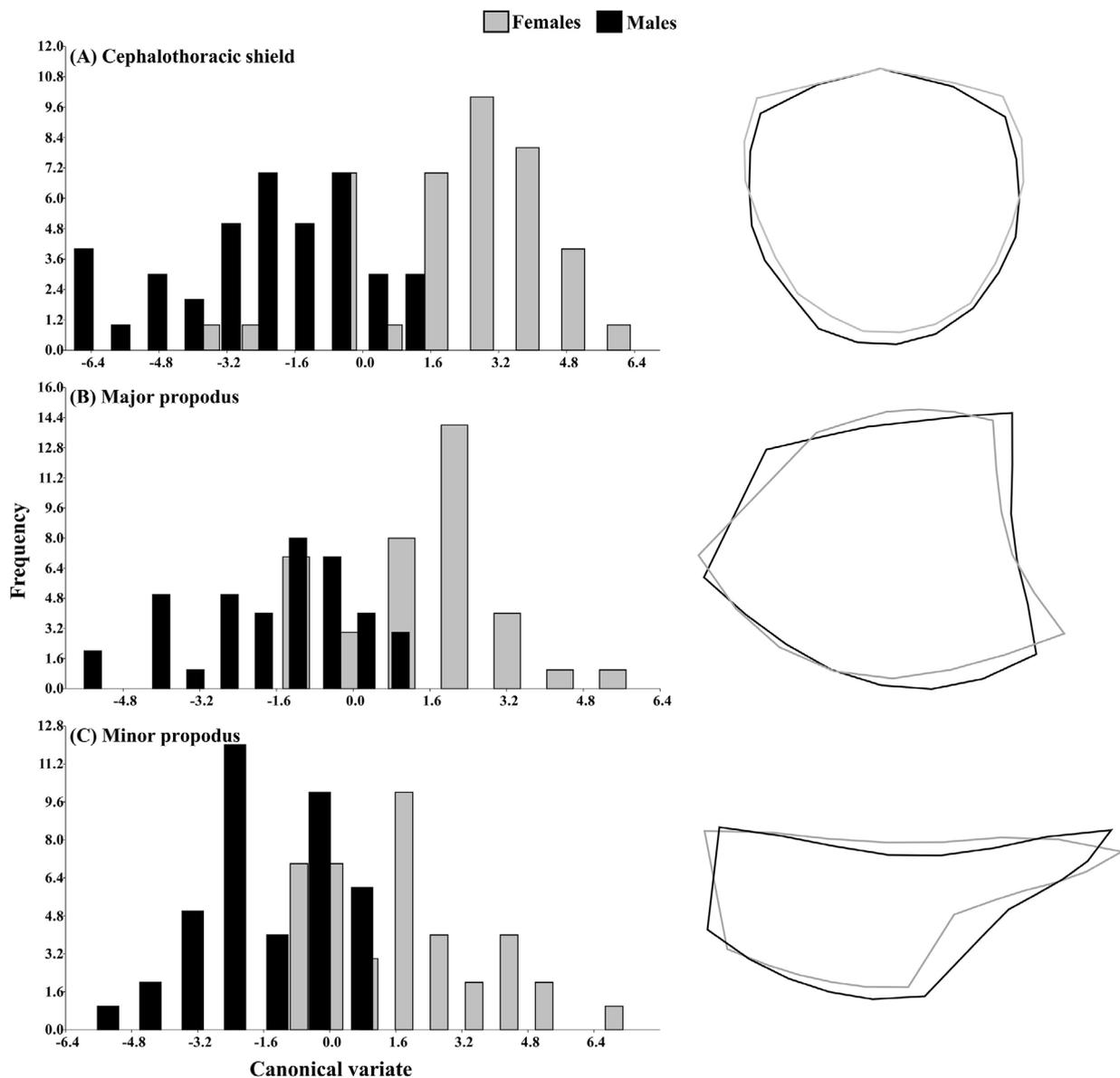
in males than in females (Fig. 2A). The variation of the MaP and MiP shapes exhibited a similar pattern. The manus region of MaP and MiP was more robust in males than in females (Fig. 2B). Furthermore, the fixed finger of the MiP was also found to be more robust in males than in females (Fig. 2C).

Sexual size dimorphism between males and females was detected in almost all structures, except CPS (t-test; $t = 1.53$, $p = 0.18$). In contrast, the size of MaP (t-test; $t = -5.99$, $p < 0.001$) and MiP (t-test; $t = -4.91$, $p < 0.001$) differed significantly between the sexes (Fig. 3A).
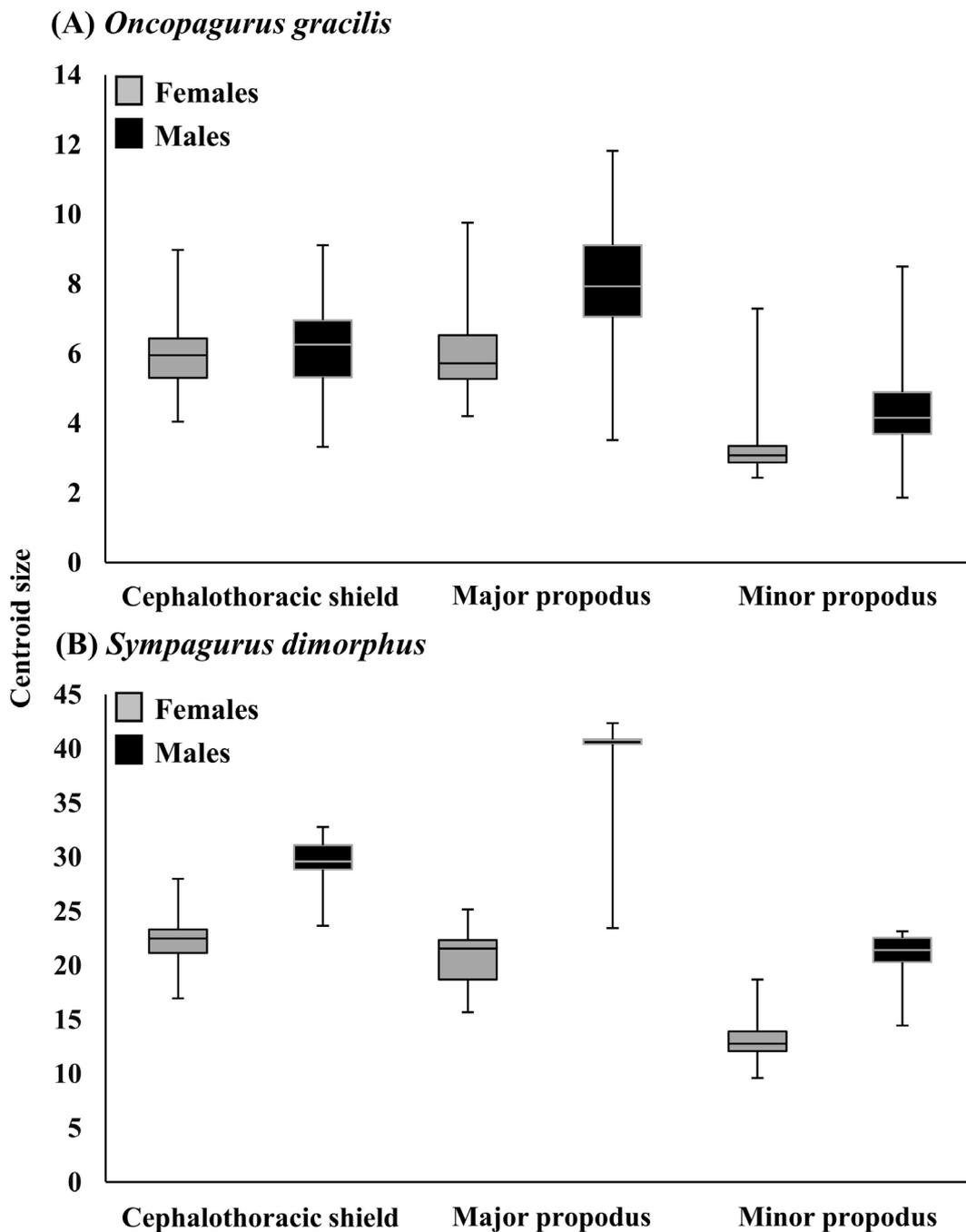
Sympagurus dimorphus

The shape of CPS (Hotelling $T^2 = 174.1$, $F = 6.59$, $p < 0.001$), MaP (Hotelling $T^2 = 101.27$, $F = 8.25$, $p < 0.001$), and MiP (Hotelling $T^2 = 70.76$, $F = 3.85$, $p < 0.001$) were different between males and females. The discriminant analysis accurately distinguished all individuals in the comparison between CPS and MaP, and about 86 % for MiP.

The frontal region of the CPS exhibited a similar shape between males and females. However, the posterior region of the CPS was wider in females than in males (Fig. 4A). In contrast, MaP was more

Figure 2. *Oncopagurus gracilis* (Henderson, 1888). Histograms and graphical representations of the shape of the structures originated from the discriminant analysis. There was low overlap between males and females in all analyzed structures.
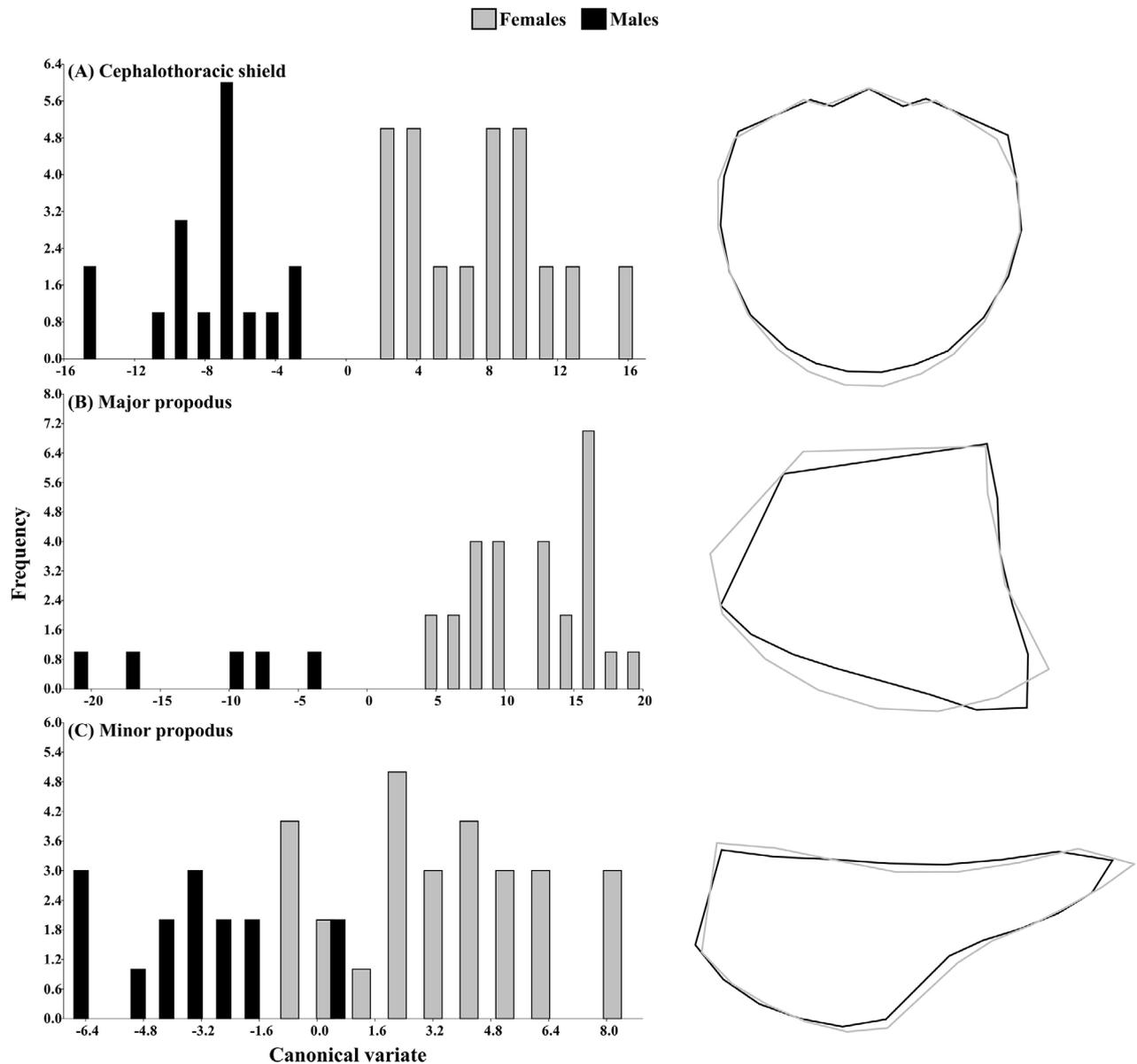
Figure 3. Comparison of the centroid size of the cephalothoracic shield, major propodus, and minor propodus between males and females of (**A**) *Oncopagurus gracilis* (Henderson, 1888) and (**B**) *Sympagurus dimorphus* (Studer, 1883). Overall, males of both species are larger than females. The size of the cephalothoracic shield of males and females of *O. gracilis* was not statistically different (*t*-test; *t* = 1.53, *p* = 0.18).

robust in females than in males. Additionally, males displayed a slight projection of the fixed finger of the MaP, while females did not exhibit this characteristic (Fig. 4B). The differences in the shape of MiP between males and females were smaller compared to the other structures. This structure was slightly more robust in females, whereas the fixed finger of males was more robust than that of females (Fig. 4C).

Sexual size dimorphism was evident between males and females in all structures analyzed, CPS (*t*-test; *t* = -9.69, *p* < 0.001), MaP (*t*-test; *t* = -9.07, *p* < 0.001), and MiP (*t*-test; *t* = -11.04, *p* < 0.001) (Fig. 3B).

Figure 4. *Sympagurus dimorphus* (Studer, 1883). Histograms and graphical representations of the shape of the structures originated from the discriminant analysis. There was low overlap between males and females only in the shape of minor propodus.

DISCUSSION

Differences in the pattern of sexual dimorphism were observed in the two species studied, in line with our initial hypotheses. Sexual size dimorphism is a common characteristic among crustaceans, where males are typically larger than females. However, deviations from this pattern have been observed in some crustaceans, which have been attributed to specific types of reproductive behaviors and mating systems (Hartnoll, 2001; Cothran and Thiel, 2020; da Silva et al., 2021). In the case of *S. dimorphus,* males

were larger than females, consistent with the typical size dimorphism pattern. However, in *O. gracilis,* no size dimorphism was observed for the cephalothoracic shield. This could be related to the availability of shells in deep-sea environments, where gastropods, although abundant, are relatively small and fragile, which may limit the growth of hermit crabs (Absalão et al., 2005; Figueira and Absalão, 2010; Abbate et al., 2022). It is known that shell availability can influence hermit crab growth (Angel, 2000; da Silva et al., 2019). Therefore, if shells are a limiting resource, male growth could be

restricted to the same size as females. Some studies on sexual size dimorphism in hermit crabs suggest that male size has a low impact on mating and female choice (Contreras-Garduño and Córdoba-Aguilar, 2006) but a high impact on male-male competition (Contreras-Garduño and Córdoba-Aguilar, 2006; Yoshino et al., 2011).

The CPS of both species exhibited shape differences between males and females, with an inverse pattern observed. In females of *S. dimorphus*, the structure displayed a more rounded posterior margin than that seen in males, whereas in males of *O. gracilis*, this structure exhibited a posterior margin that was more rounded than that seen in females. In crustaceans with an advanced carcinization process, it is common to observe females carrying a carapace with a more robust shape than males due to the repositioning of the abdomen in relation to the body and the larger abdomen size in females (Trevisan et al., 2012; Keiler et al., 2017; Marochi et al., 2019; da Silva et al., 2021; Wolfe et al., 2021). Therefore, due to the ventral location of the abdomen in the animal's body, which is connected to the posterior region of the carapace, modifications occur in the carapace to support the weight of the robust abdomen (Marochi et al., 2019; Wolfe et al., 2021). Thus, hermit crabs, which lack advanced carcinization and possess a non-calcified abdomen, are not expected to exhibit this type of variation (Keiler et al., 2017). The observed variation in the CPS shape in *S. dimorphus* and *O. gracilis* may be related to the specific allometric constants that determine the size and shape of the CPS of males and females of each species, as highlighted for the hermit crab *Clibanarius signatus* Heller, 1861 (Ismail, 2018).

The claws of both species, MaP and MiP, exhibited sexual size dimorphism, with males displaying larger claws than females. This phenomenon is commonly observed in crustaceans, where the larger claw is frequently linked to resource competition (Turra and Denadai, 2004; Almerão et al., 2010; Kruesi et al., 2022; Nogueira et al., 2022). In hermit crabs, such contests can pertain to food, mates, and/or shell acquisition (Turra and Denadai, 2004; Yoshino et al., 2011; Quinn, 2020). Hence, the selective pressures associated with these contests may influence claw size, thereby resulting in the observed differences between both species (Dennenmoser and Christy,

2013; Palaoro et al., 2020; Levinton and Weissburg, 2021; Nogueira et al., 2022). Given that males possess larger claws, they are likely to generate more force using their claws (Schenk and Wainwright, 2001; Claussen et al., 2008), which is an advantageous trait during competitions for resources or mates. Additionally, claws can also play a signaling role in a "pre-fight" scenario, intimidating potential opponents. In some instances, individuals tend to refrain from initiating a fight if their opponents possess large weapons. Prior to engaging in combat, a display phase may occur, where males showcase their claws to each other, and if one of the competitors assesses that the energy cost involved in the fight exceeds its potential gain, the individual may flee, thus avoiding combat (Parra et al., 2011; Palaoro et al., 2020).

As mentioned above, competition for shells in *S. dimorphus* is low, hence the selective pressure on claws in this species is also expected to be low. Nevertheless, differences in size and shape of claws between males and females have been observed. Thus, we can propose an alternative hypothesis for the occurrence of this dimorphism, which may be related to some genetic factor involved in the development of the cheliped. This could be attributed to the claw development not being linked to sex genes, allowing this structure to develop and grow, attaining ideal shapes and sizes for both sexes (Bondurizansky, 2007; Bonduriansky and Chenoweth, 2009).

The shape of the major cheliped (MaP) varied between males and females of both species, but there was an inverse pattern between the two species. In *S. dimorphus*, females presented a more robust MaP, whereas in *O. gracilis*, males exhibited a more robust MaP. *Oncopagurus gracilis* follows the typical pattern observed in crustaceans, where males possess more robust claws than females (Mariappan et al., 2000; Nirmal et al., 2020). In hermit crabs, claws serve multiple functions, including food acquisition and shell-fighting. In the latter scenario, hermit crabs use their claws to grab their opponents' shells and repeatedly hit them against their own shell, causing their opponent to exit their shell. This aggressive behavior is referred to as rapping (Lane and Briffa, 2020; Lane et al., 2022). The claw also plays a crucial role in mating-related behaviors. For instance, inverse rapping behavior (Kido and Wada, 2020) and male

hermit crabs protecting females during the pre-mating phase (Yoshino et al., 2004; Contreras-Garduño and Córdoba-Aguilar, 2006) involve the use of the claw. Furthermore, males use their claws to reach females inside the shells and drag them out for forced copulation (Yoshino et al., 2004). Thus, a claw with a robust shape is likely advantageous for male hermit crabs, as it facilitates their performance in diverse tasks.

Sympagurus dimorphus is primarily found inhabiting zoanthid colonies, although occasionally larger males can be observed using gastropod shells as shelter (Schejter and Mantelatto, 2011). The frequent use of zoanthids as shelter implies that shell fighting may not be a crucial factor for this species, which has resulted in a dimorphic pattern where females possess a more robust and rounded claw while males have a spear-shaped claw. Males of *S. dimorphus* may exhibit unique behavioral traits that influence the shape of their MaP. However, it is essential to carry out experiments that detail the behavioral repertoire of these organisms to confirm this hypothesis. Nevertheless, conducting such experiments can be challenging due to the difficulty in collecting and rearing these animals in a controlled environment, given the pressure of their natural habitat.

The variation in shape of the MiP was similar between the two species, with males presenting a more robust MiP compared to females. Although this structure is less frequently used during agonistic events, it remains important, particularly for hermit crabs, due to their rapping and inverse rapping behaviors (Dowds and Elwood, 1983; Kido and Wada, 2020). As previously mentioned, some male hermit crabs exhibit pre-copulatory behavior known as inverse rapping, whereby they hold the female's shell with both claws and hit it against their own shell (Kido and Wada, 2020). Thus, possessing a more robust and stronger MiP can facilitate the execution of these movements, and ensure the reproductive success of these organisms. This highlights the critical importance of this structure in the life history of hermit crabs.

This study presents novel and complementary information on sexual dimorphism in two species of hermit crabs from the family Parapaguridae, which is less studied compared to other families such as Paguridae and Diogenidae. We observed that one of the studied species, *S. dimorphus*, exhibited shape variations that deviate from the general crustacean pattern, likely related to its habitat and the adaptive processes it underwent to thrive in an environment with limited shelter availability. Furthermore, our findings highlight the importance of claws for hermit crabs, as both propodi displayed variations in size and shape that follow a similar trend, potentially related to their use during agonistic events as observed in other hermit crab species (Lane and Briffa, 2020; Lane et al., 2022). Finally, we emphasize the need for further studies on other populations and species of Parapaguridae to facilitate comparative analyses.

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ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Conceptualization and Design: ARdS, LS. Performed research: AC, CSN, ARdS. Acquisition of data: AC, LS, ARdS. Analysis and interpretation of data: AC, ARdS, CSN. Preparation of figures: CSN. Writing original draft: AC, CSN. Writing - critical review & editing: ARdS, LS, CSN.

Consent for publication

All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

Competing interests

The authors report there are no competing interests to declare.

Data availability

The data that support the findings of this study are available from the corresponding author, ARdS, upon reasonable request.

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